Far Eastern Entomologist
Дальневосточный энтомолог

Journal published by Far East Branch of the Russian Entomological Society and Laboratory of Entomology, Federal Scientific Center of the East Asia Terrestrial Biodiversity, Vladivostok

Number 427: 1-19 | ISSN 1026-051X (print edition) ISSN 2713-2196 (online edition) | March 2021

https://doi.org/10.25221/fee.427.1
http://zoobank.org/References/8C87C596-7C5F-4083-9A63-8C3D33F5DCA9

TWO NEW NEARCTIC GENERA IN THE TRIBE ODYNERINI S. STR. REVEALED ON THE BIONOMICS AND MORPHOLOGY, WITH A COMMENT ON THE COCOONS OF THE EUMENINE WASPS (HYMENOPTERA: VESPIDAE: EUMENINAE)

A. V. Fateryga

T.I. Vyazemsky Karadag Scientific Station – Nature Reserve of RAS – Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Kurortnoye, Feodosiya, 298188, Russia. E-mail: fater_84@list.ru

Summary. Two new genera are described for three species in the "red" group of the North American eumenine wasps from the genus *Odynerus* Latreille, 1802: *Bohartodynerus* Fateryga, **gen. n.** for *O. margaretellus* Rohwer, 1915 (type species) and *O. cinnabarinus* Bohart, 1939, and *Parkerodynerus* Fateryga, **gen. n.** (type species *O. erythrogaster* Bohart, 1939). *Bohartodynerus cinnabarinus* **comb. n.** is newly recorded from Nevada and New Mexico and *B. margaretellus* **comb. n.** from California, New Mexico, Utah, and Wyoming. Bionomics of the species included to these genera are summarized. Nectar robbing is reported for wasps in the genus *Bohartodynerus* at flowers of *Astragalus* spp. (Fabaceae), *Penstemon* sp. (Plantaginaceae), and *Calylophus* sp. (Onagraceae). It is speculated that nectar is used by them to bond the gravel during the construction of the closing plug of the nest. *Parkerodynerus erythrogaster* **comb. n.** apparently does not use liquid for the nest construction. Bionomics of other genera in the *Odynerus* group of the tribe Odynerini s. str. are discussed. Neither *Bohartodynerus* nor *Parkerodynerus* can be treated as members of the genus *Odynerus* according to their ethology, and the differences between these two newly described taxa are also enough to recognize them as separate genera. A cocoon of *P. erythrogaster* is described in detail; it has a sandwich-like structure with two layers of silk strands and a layer of sand

in-between. Similar structure is found in the cocoons of other genera in the *Odynerus* group but only at the free part of the cocoon instead over its whole surface; that was overlooked during the previous studies of those genera.

Key words: *Odynerus*, taxonomy, distribution, nesting habits, nectar robbing, cocooning behavior, Nearctic region.

А. В. Фатерыга. Два новых неарктических рода трибы Odynerini s. str., выделенные на основании биологии и морфологии, с замечанием по коконам ос-эвменин (Hymenoptera: Vespidae: Eumeninae) // Дальневосточный энтомолог. 2021. N 427. С. 1-19.

Резюме. Описано два новых рода для трёх североамериканских видов из группы «красных» ос-эвменин из рода *Odynerus* Latreille, 1802: род *Bohartodynerus* Fateryga, **gen. n.** для *O. margaretellus* Rohwer, 1915 (типовой вид) и *O. cinnabarinus* Bohart, 1939 и *Parkerodynerus* Fateryga, **gen. n.** (типовой вид *O. erythrogaster* Bohart, 1939). *Bohartodynerus cinnabarinus* **comb. n.** приводится впервые для Невады и Нью Мехико; *B. margaretellus* **comb. n.** – для Калифорнии, Нью Мехико, Юты и Вайоминга. Обобщена биология видов, включенных в эти роды. Для ос рода *Bohartodynerus* сообщаются случаи воровства нектара на цветках *Astragalus* spp. (Fabaceae), *Penstemon* sp. (Plantaginaceae) и *Calylophus* sp. (Onagraceae). Предполагается, что нектар используется ими для скрепления мелких камешков при строительстве конечной пробки гнезда. *Parkerodynerus erythrogaster* **comb. n.**, по-видимому, не использует жидкость для строительства гнезда. Обсуждается биология других родов трибы Odynerini s. str. из группы *Odynerus*. Согласно этологическим признакам, ни *Bohartodynerus*, ни *Parkerodynerus* не могут рассматриваться в составе рода *Odynerus*; различия между двумя описанными таксонами также достаточны для того, чтобы признавать их самостоятельными родами. Подробно описан кокон *P. erythrogaster*, имеющий строение, подобное сандвичу: два слоя шелковых нитей и слой песка между ними. Сходное строение кокона обнаружено также у других родов из группы *Odynerus*, но только в свободной части кокона, а не по всей его поверхности; данная особенность была упущена в ходе предыдущих исследований этих родов.

INTRODUCTION

Bohart (1939) revised the genus *Odynerus* Latreille, 1802 (as the subgenus *Odynerus* s. str.) in North America with five species included: *O. aldrichi* Fox, 1892, *O. dilectus* de Saussure, 1870, *O. erythrogaster* Bohart, 1939, *O. margaretellus* Rohwer, 1915, and *O. cinnabarinus* Bohart, 1939. The first species was later moved by him to a genus *Pseudepipona* de Saussure, 1856, as *P. herrichii aldrichi* (Fox, 1892) (Bohart, 1951), which is phylogenetically distant (Bank *et al*., 2017; Piekarski *et al*., 2018), while four others were treated as members of the genus *Odynerus* (subgenus *Odynerus* s. str.) till present. Among them, *O. dilectus* is closely related to the type species of the genus, Palaearctic *O.* (*Odynerus*) *spinipes* (Linnaeus, 1758), and has similar bionomics. Females of *O. dilectus* nest in the ground where they excavate burrows with the aid of water; the nest entrance is surmounted by a mud turret (= chimney); the provision is free-living curculionid larvae (Bohart *et al*., 1982; Schaber, 1985). Three remaining species represent a complex of “red” wasps with remarkable habitus (Figs 1, 21–23). They are quite different from both *O. dilectus* and all the numerous Palaearctic members of the genus by both morphology and bionomics. The nesting of two species in this

"red" complex was studied in detail by Parker (1984). According to him, they use pre-existing cavities in twigs, do not use water, and do not construct entrance turrets; their provision is lepidopteran larvae (caterpillars).

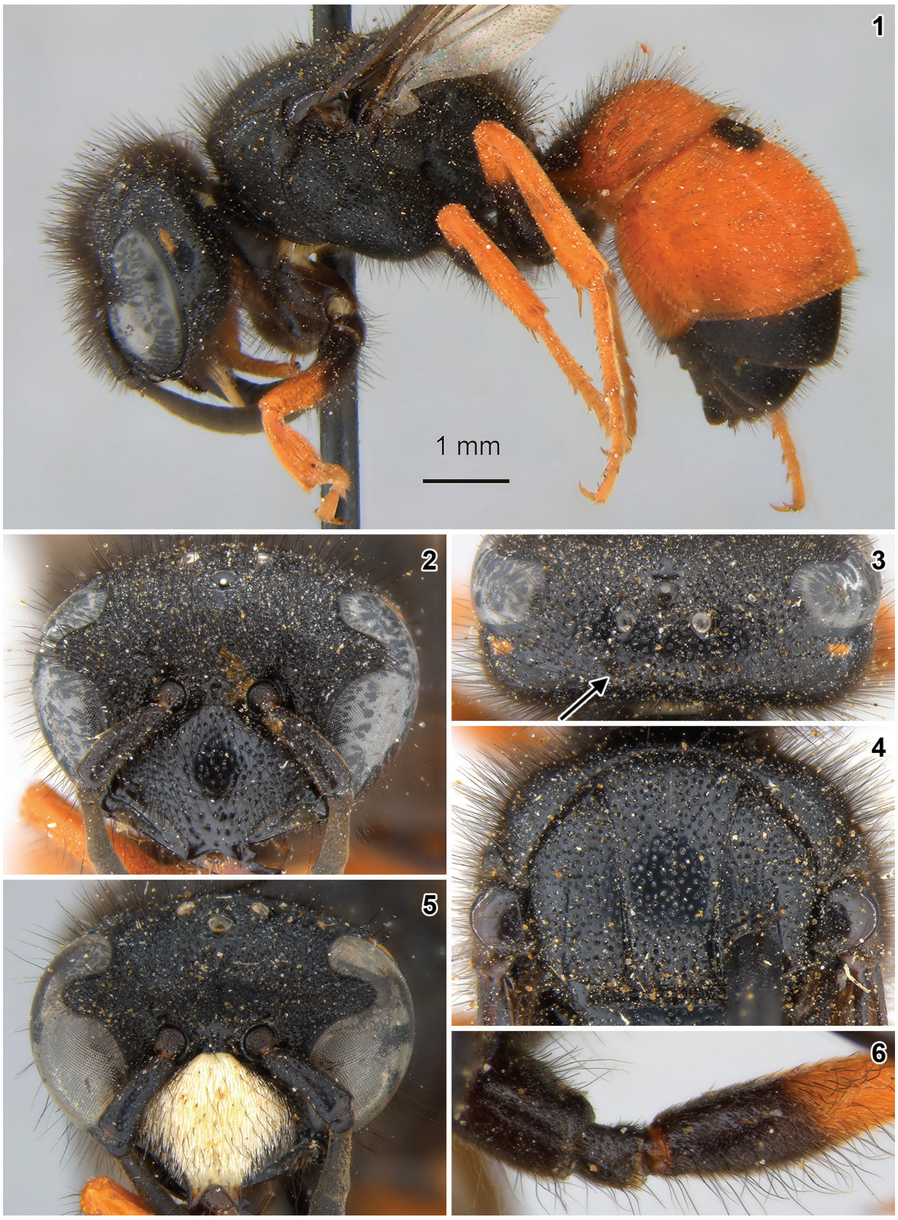
At the same time, Blüthgen (1938a, 1938b, 1939, 1941), working with the Palaearctic eumenine wasps, was remarkably more "splitting" than Bohart. He segregated from the genus *Odynerus* (as *Hoplomerus* Agassiz, 1846) several subgenera (*Monoplomerus* Blüthgen, 1941 and *Spinicoxa* Blüthgen, 1938) and separate genera (*Gymnomerus* Blüthgen, 1938, *Paragymnomerus* Blüthgen, 1938, *Paravespa* Radoszkowski, 1886, and *Tropidodynerus* Blüthgen, 1939). At least a half of these names (*Spinicoxa*, *Gymnomerus*, and *Paragymnomerus*) were treated as synonyms of *Odynerus* by Bohart (1951). Parker (1966), revising another genus *Leptochilus* de Saussure, 1853, generally criticized the "splitting" generic system accepted by Blüthgen for the eumenine wasps at all, but at the same time he was first who suggested the artificiality of the genus *Odynerus* in its treatment by Bohart (1951). He wrote: "To illustrate one of many instances of the generic confusion, one should examine the 4 Nearctic species that are placed in *Odynerus*. When these species are critically examined, it is found that they form 2 natural groups which are easily separated by morphological and biological differences" (Parker, 1966: 156).

Working with the collection of the Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far East Branch of the Russian Academy of Sciences, Vladivostok, Russia [FSCV] in 2019, I found two specimens of *O. erythrogaster* reared by Parker, with their cocoons pinned under them. Studying these cocoons with an attempt to receive some more information than Parker (1984) published; I also paid an attention to the morphology of the wasps themselves and found that they significantly differed from both typical *Odynerus* and two other species in the "red" complex. Therefore, this complex proved to require a further subdivision. The purpose of the present study is to propose a new generic classification of the North American species hitherto included to the "red" complex of *Odynerus* and to summarize their distribution and bionomics. In addition, I am taking this opportunity to comment my previous incomplete (and partially incorrect) descriptions of the cocoons of some species in the related genera *Tropidodynerus* (Fateryga, 2009), *Gymnomerus* (Fateryga, 2012), *Odynerus* (Fateryga, 2013), *Paravespa* (Fateryga & Ivanov, 2013), and *Paragymnomerus* (Fateryga, 2018).

MATERIAL AND METHODS

Specimens of the studied complex of wasps were examined in FSCV as well as in the collection of the California Department of Food and Agriculture, Sacramento, USA [CDFA] via high quality photos kindly provided by Kevin A. Williams. Specimens of other related genera were examined in the research collection of the author and partly in FSCV.

Photographs were taken in FSCV with an Olympus DP74 digital camera attached to an Olympus SZX16 stereomicroscope. Multifocus-images were created from stacks of photographs using Helicon Focus 6 Pro software. Final illustrations were postprocessed for sharpness, contrast, and brightness using Adobe Photoshop CS2 software. Male genitalia were extracted after re-softening the specimens and were then boiled in 10% NaOH for 5 min. After that, they were rinsed in 80% ethanol and only then stored and studied in glycerin. The drawings were made on graph paper with the aid of an ocular square grid; final drawings were made by outlining the draft drawings. SEM micrographs of the cocoons were taken using a Hitachi SE3500 Scanning Electron Microscope. The cocoon fragments were not critical-point dried; they were simply mounted on stubs and coated with gold and palladium.



Figs 1–6. *Bohartodynerus margaretellus* (Rohwer, 1915): 1–4 – female (1 – habitus, lateral view; 2 – head, frontal view; 3 – head, dorsal view, arrow indicates a cephalic fovea; 4 – pronotum and scutum); 5, 6 – male (5 – head, frontal view; 6 – mid leg beneath). Photos by K.A. Williams.

The morphological terminology is based on Yamane (1990). Distribution of the species is listed according to Krombein (1979), with some additions reported by Parker (1984), and according to the material examined and the data from the BugGuide web-site (https:// bugguide. net/). Hitherto unpublished records are marked with an asterisk (*).

It is worthy to clarify the terminology dealing with the classification of the eumenine wasps due to the differences between the traditional (Carpenter, 1982; Hermes *et al*., 2014) and the molecular (Bank *et al*., 2017; Piekarski *et al*., 2018) phylogenetic approaches. Hermes *et al*. (2014) subdivided the subfamily Eumeninae to three tribes: Zethini, Eumenini, and Odynerini. Molecular data (Bank *et al*., 2017; Piekarski *et al*., 2018) suggested recognizing Zethini sensu Hermes *et al*. (2014) as two separate subfamilies: Raphiglossinae and Zethinae. Furthermore, the tribe Odynerini sensu Hermes *et al*. (2014) proved to be paraphyletic to Eumenini according to Bank *et al*. (2017) and Piekarski *et al*. (2018) who revealed that the "molecular" Eumeninae (without Zethinae and Raphiglossinae) consisted of five main clades. Therefore, to avoid confusion, I propose using the following terms: Eumeninae s. l. (Eumeninae sensu Carpenter, 1982 and Hermes *et al.*, 2014), Eumeninae s. str. (Eumeninae sensu Bank *et al*., 2017 and Piekarski *et al*., 2018), Odynerini s. l. (Odynerini sensu Hermes *et al*., 2014), and Odynerini s. str. (one of the five "molecular" clades of Eumeninae s. str. containing the genus *Odynerus*).

Members of Odynerini s. str. are characterized, first of all, by a small, posteriorly rounded tegula that is considered as apomorphic state (Carpenter & Cumming, 1985). There are two main artificial groups of Odynerini s. str.: the *Odynerus* group (genera with four labial palpomeres) and the *Pterocheilus* group (genera with three labial palpomeres). The former group is apparently paraphylectic to the latter one while the latter group is probably polyphyletic. The *Odynerus* group contains the genera *Odynerus*, *Gymnomerus*, *Paragymnomerus*, *Paravespa*, and *Tropidodynerus*. The *Pterocheilus* group contains the genera *Pterocheilus* Klug, 1805, *Aethiopicodynerus* Gusenleitner, 1997, *Cephalochilus* Blüthgen, 1939, *Hemipterochilus* Ferton, 1909, *Megapterocheilus* Bohart, 1940, *Micropterocheilus* Bohart, 1940, *Onchopterocheilus* Bohart, 1940, *Onychopterocheilus* Blüthgen, 1955, and probably *Pseudochilus* de Saussure, 1856 (the latter one was not examined by the author). The genus *Pteromenes* Giordani Soika, 1960 apparently does not belong to Odynerini s. str. and possesses a similar tegula due to a homoplasy. At the same time, according to Bank *et al*. (2017), the clade of *Odynerus* contains also some little-known genera with the tegula emarginate adjoining the parategula (plesiomorphic state according to Carpenter & Cumming, 1985), such as *Pseudoleptochilus* Blüthgen, 1938 and *Pseudosymmorphus* Blüthgen, 1938 (both were not examined by the author), which are sister to all the remaining genera (i. e., the *Odynerus* and *Pterocheilus* groups) in this clade.

TAXONOMY

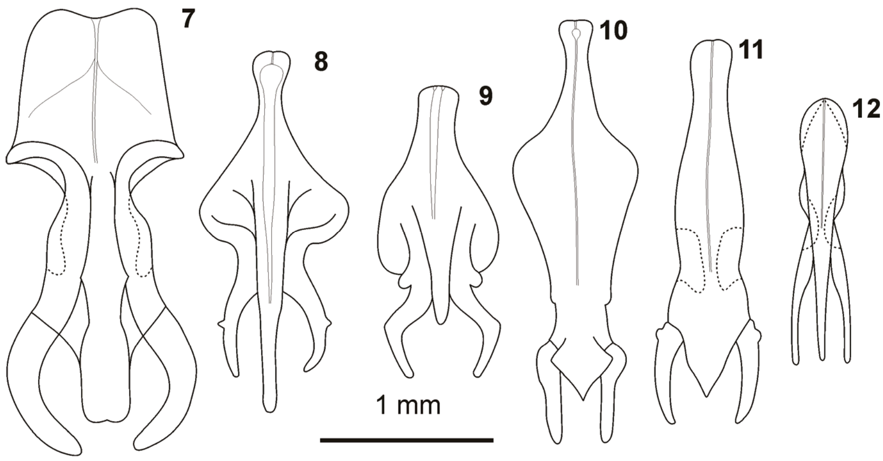
Genus *Bohartodynerus* Fateryga, gen. n.

http://zoobank.org/NomenclaturalActs/84A450D8-4E9B-4B62-934E-8FC1C5BC1CEF

Type species: *Odynerus margaretellus* Rohwer, 1915, here designated.

DIAGNOSIS. The new genus belongs to the *Odynerus* group of Odynerini s. str. It can be distinguished from the genus *Odynerus* by a narrow apical margin of the clypeus (Figs 2, 5) with acute lateral teeth in both sexes (broad margin in both sexes with rounded teeth in the female in *Odynerus*, Figs 13, 16, 17), the absence of distinct pronotal foveae and the pronotal carina (both present in *Odynerus*), sharply impressed notauli and distinct parapsidal

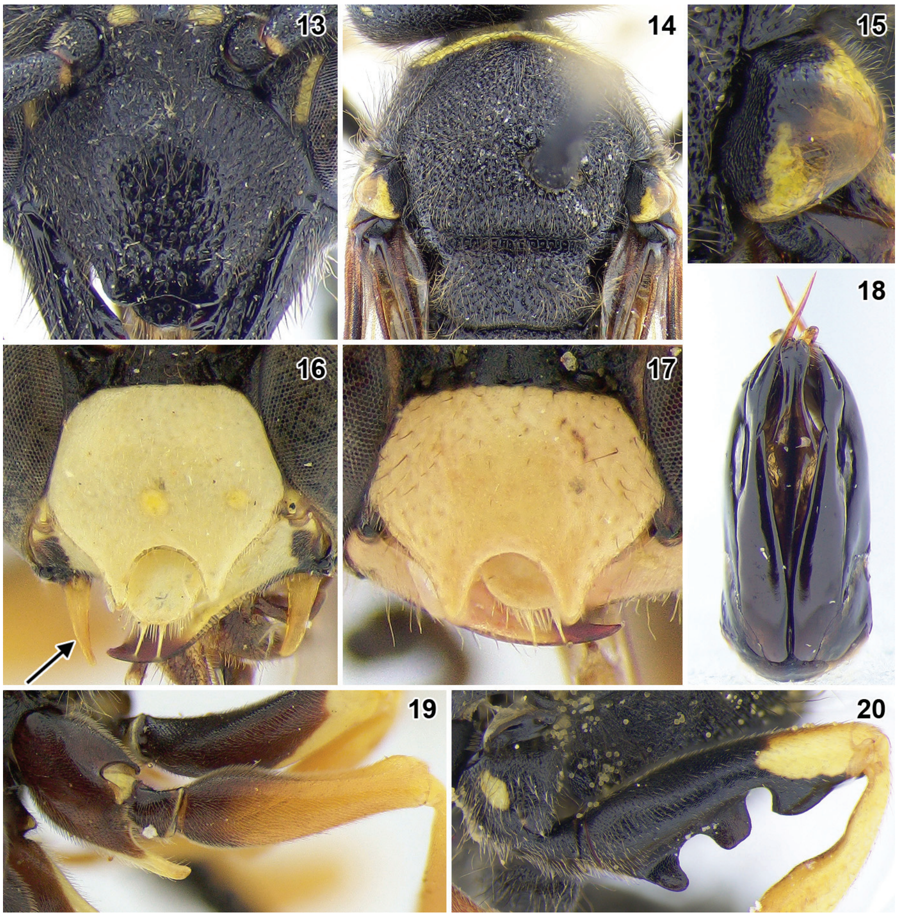
lines (Fig. 4) (both absent in *Odynerus*, Fig. 14, but present also in *Paravespa*), the tegula with a small but evident inner posterior angle where it adjoins the scutum (completely rounded posteriorly in *Odynerus*, Fig. 15), the presence of an epicnemial carina (absent in *Odynerus*), a dense short pilosity of the posterior sterna in the male (absent in *Odynerus* but present in *Tropidodynerus* and some *Paragymnomerus*), and a broad, greatly expanded and truncate apex of the male aedeagus (Bohart, 1939: 79, fig. 3) (present also in *Paravespa*, Fig. 7). Furthermore, males of *Odynerus* have either a projection on the gena behind the mandible or on the mid coxa (subgenus *Spinicoxa*, Figs 16, 19), or an extraordinarily notched mid femur (subgenus *Odynerus* s. str., Fig. 20), or a sharp edge of the fore femur beneath (subgenus *Monoplomerus*). Male genitalia of *Odynerus* (Fig. 18) are also very different from *Bohartodynerus* gen. n.; the shape of the aedeagus in *Gymnomerus* (Fig. 9) is rather similar to that in *Odynerus* (Fig. 8), while it is also distinctly different in *Paragymnomerus* (Fig. 10) and *Tropidodynerus* (Fig. 11).



Figs 7–12. Aedeagus, dorsal view: 7 – *Paravespa* (*Paravespa*) *quadricolor* (Morawitz, 1885); 8 – *Odynerus* (*Odynerus*) *spinipes* (Linnaeus, 1758); 9 – *Gymnomerus laevipes* (Shuckard, 1837); 10 – *Paragymnomerus signaticollis* (Morawitz, 1888); 11 – *Tropidodynerus* (*Tropidodynerus*) *interruptus* (Brullé, 1832); 12 – *Parkerodynerus erythrogaster* (Bohart, 1939).

DESCRIPTION. *Female.* Head about 1.2 as wide as long in frontal view; clypeus about 1.2 as wide as long, with shallow apical emargination as wide as distance between antennal foveae, apical teeth acute (Fig. 2). Mandible without notch. Proboscis short, not reaches mid coxae. Maxillar palpi with 6 articles; labial palpi with 4 articles. Vertex longer than upper portion of compound eye in dorsal view; cephalic foveae small and shallow or indistinct, separated by distance somewhat larger than that between lateral ocelli (Fig. 3). Anterior face of pronotum without distinct foveae; pronotal carina absent; pronotum beneath without acute angle anteriorly. Notauli sharply impressed, running entire length of scutum; parapsidal lines present on distal 2/3 of scutum; scutum evenly punctured (Fig. 4). Tegula small, nearly rounded posteriorly but with evident inner posterior angle where it adjoins scutum; parategula very small. Epicnemial carina present. Scutellum convex; axillary fossa deep. Metanotum rounded posteriorly. Propodeal shelf not developed. Propodeal concavity rather flat, its lateral borders

rounded. Propodeal valvula entire. Second submarginal cell of fore wing not petiolate, with acute basal angle. Parastigma shorter than pterostigma. Tergum 1 hardly petiolate, without transverse carina at summit and without apical furrow. All metasomal terga without apical lamellae. Sternum 2 without distinct basomedian longitudinal sulcus. Black wasps with reddish pattern and erect, long, mostly dark pilosity (Fig. 1).



Figs 13–20. *Odynerus* spp.: 13–15 – *O.* (*Odynerus*) *spinipes* (Linnaeus, 1758), female (13 – clypeus; 14 – pronotum and mesonotum; 15 – tegula); 16, 19 – *O.* (*Spinicoxa*) *renifo-rmis* (Gmelin, 1790), male (16 – clypeus, arrow indicates a genal projection; 19 – mid leg beneath); 17 – *O.* (*O.*). *dilectus* de Saussure, 1870, male, clypeus; 18, 20 – *O. spinipes*, male (18 – genitalia, dorsal view; 20 – mid leg beneath). Photos by M.Yu. Proshchalykin.

Male. Resembles female but clypeus with deeper apical emargination and covered with pale appressed setae besides erect dark pilosity (Fig. 5). Gena without projection behind mandible. Antenna with flagellomere 10 much shorter than flagellomere 11; apex of antenna forming hook (Bohart, 1939: 79, fig. 11) or loose coiling. Fore femur beneath without sharp edge. Mid leg with neither projection on coxa nor any unusual structures on femur (Fig. 6).

Sterna 3–6 with dense short pale pilosity. Aedeagus very broad, greatly expanded and truncate apically (Bohart, 1939: 79, fig. 3).

ETYMOLOGY. The new genus-group name is dedicated to Richard M. Bohart (1913–2007), a famous entomologist, for his significant contributions to the taxonomy and systematics of the American eumenine wasps. The gender is masculine.

SPECIES INCLUDED. *Bohartodynerus cinnabarinus* (Bohart, 1939), **comb. n.** and *B. margaretellus* (Rohwer, 1915), **comb. n.**

DISTRIBUTION. Nearctic region (USA).

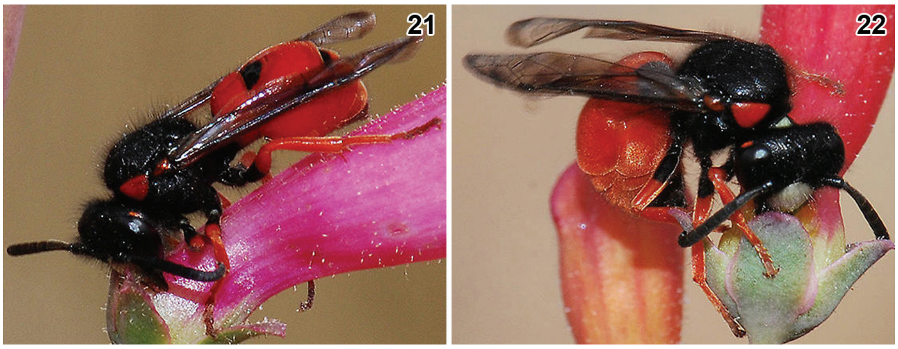
***Bohartodynerus cinnabarinus* (Bohart, 1939), comb. n.**

Figs 21, 22

Odynerus cinnabarinus Bohart, 1939: 83–84, ♀♂ (type locality: "Beaver Creek Hills, Beaver County, Utah" [USA]), holotype, ♂, in the collection of the California Academy of Sciences, San Francisco, USA.

DISTRIBUTION. USA (Arizona, California, *Nevada, *New Mexico, Texas, Utah).

REMARKS. No material was examined. The records from Nevada and New Mexico are added according to the BugGuide web-site (e. g., https://bugguide.net/node/view/1296202 and https://bugguide.net/node/view/256663).



Figs 21–22. A male of *Bohartodynerus cinnabarinus* (Bohart, 1939) robbing nectar from a flower of *Penstemon* sp. (probably *P. alamosensis* Pennell & G.T. Nisbet) through a hole gnawed out by itself with the mandibles in the corolla tube. Photos by R.D. Barber from the BugGuide web-site (https://bugguide.net/node/view/256663 and https://bugguide.net/node/view/ 256665), distributed under the terms of the Creative Commons BY-ND-NC 1.0 license (https://creativecommons.org/licenses/by-nd-nc/1.0/).

BIONOMICS. Parker (1984) reported a nest of this species made in a side hole drilled in a pithy stem (the hole were slightly widened and lengthened by the female wasp). He also speculated that the species may nest in stone caverns. The described nest had a single cell sealed with the closing plug which "consisted of several large sand grains that were held in place by smaller pieces and liquid substance" (Parker, 1984: 524). Fateryga & Podunay (2018) supposed that this liquid substance was actually nectar. Indeed, the described closing plug appears similar to that of *Alastor* (*Alastor*) *mocsaryi* (André, 1884), a species which proved to use nectar for the nest construction (Fateryga & Podunay, 2018). It was also speculated that the use of nectar is correlated with its robbing from the flowers by gnawing holes in the

perianth (Fateryga *et al*., 2020). *Bohartodynerus cinnabarinus* is a common nectar robber. It is known gnawing the holes in calyces of *Astragalus holmgreniorum* Barneby (Fabaceae) (Barlow & Pavlik, 2017) and corollas of *Penstemon* sp. (Plantaginaceae) (Figs 21, 22). There is also a photo of apparently this species robbing nectar from a calyx tube of a flower of *Calylophus* sp. (Onagraceae). (https://www.inaturalist.org/observations/26950910).

Provision of *B. cinnabarinus* is lepidopteran caterpillars (Parker, 1984). Parker also reported that the cocoon of this species "was similar to that of *O. erythrogaster* (sand and silk)" (Parker, 1984: 523), which will be described below.

***Bohartodynerus margaretellus* (Rohwer, 1915), comb. n.**
Figs 1–6

Odynerus margaretellus Rohwer, 1915: 242–243, ♀♂ (type locality: "Troublesome, Colorado" [USA]), holotype, ♀ (no. 18526), in the collection of the Smithsonian National Museum of Natural History, Washington, D.C., USA.

MATERIAL EXAMINED. **USA:** *California*: Inyo County, Sierra Nevada Mountains, Coyote Ridge, 10 300–11 200′, 11.VII 1981, 1 ♀, leg. G. Giuliani [CDFA]. *Utah*: Tooele County, 4 Mi NE Camel Back Mountain, on *Astragalus* sp., 26.IV 1954, 1 ♀, leg. J. Eastin [CDFA]. *Wyoming*: Sweetwater County, Covey's Little America, 7.VI 1955, 1 ♂, leg. G.E. Bohart [CDFA]. *Washington*: Yakima County, N Yakima, 27.V 1903, 1 ♀, leg. E. Jenne [FSCV].

DISTRIBUTION. USA (*California, Colorado, *New Mexico, Oregon, *Utah, *Wyoming, Washington).

REMARKS. The record from New Mexico is added according to the BugGuide web-site (https://bugguide.net/node/view/1516898).

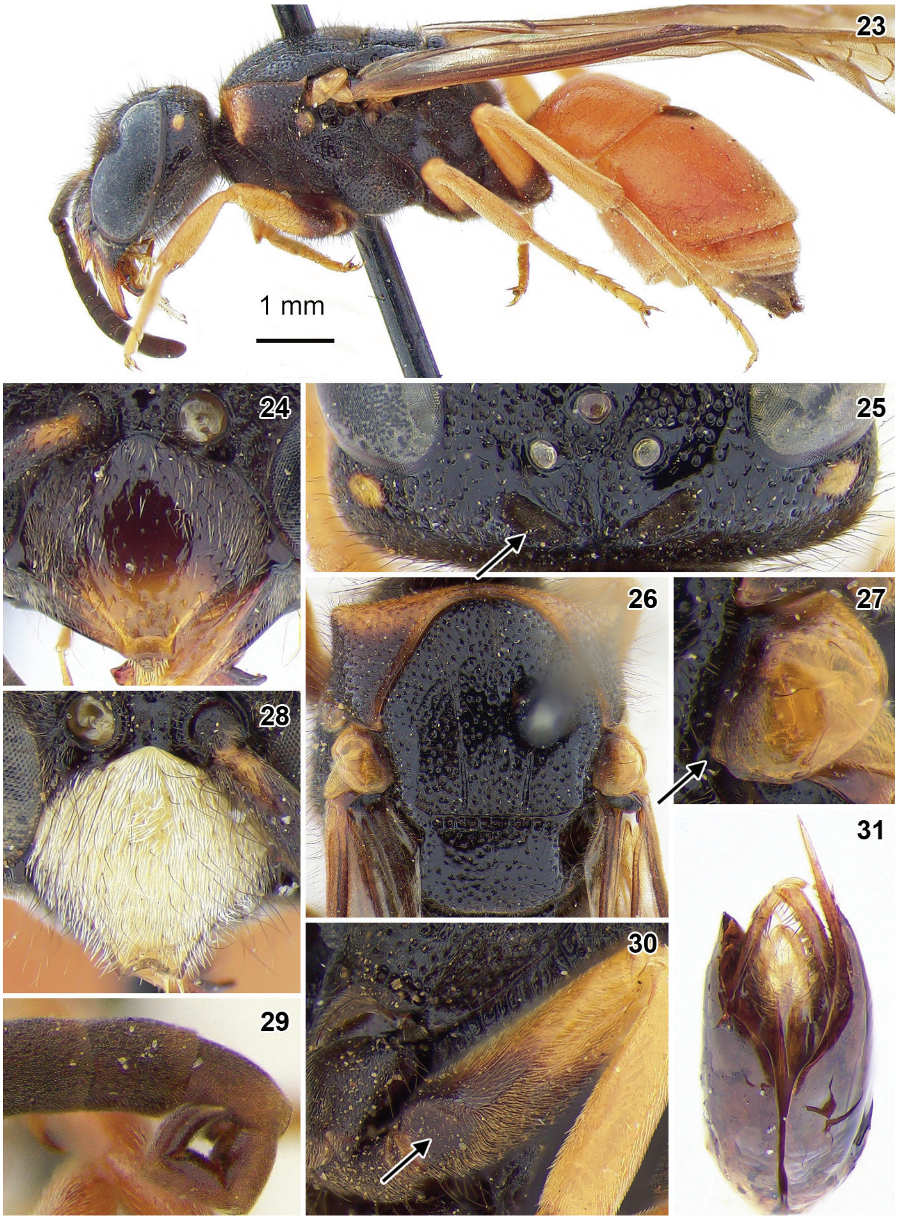
BIONOMICS. Apparently, there are no published data on the bionomics of *B. margaretellus*. The record of a female on *Astragalus* sp. allows speculating that it is also a nectar-robbing species, similarly to *B. cinnabarinus* (since all species of this plant genus have a long calyx tube and thus nectar is located much deeper than the length of the proboscis of the most eumenine wasps).

Genus *Parkerodynerus* Fateryga, gen. n.

http://zoobank.org/NomenclaturalActs/87229E9E-360A-49EC-9DD2-C9070C9101CA

Type species: *Odynerus erythrogaster* Bohart, 1939, here designated.

DIAGNOSIS. The new genus is closely related to *Bohartodynerus* gen. n. and can be also distinguished from the genus *Odynerus* by a narrow apical margin of the clypeus, the absence of distinct pronotal foveae, sharply impressed notauli and distinct parapsidal lines, the tegula with a small but evident inner posterior angle where it adjoins the scutum, a dense short pilosity of the posterior sterna in the male, a different structure of the male genitalia, and a reddish pattern. At the same time, *Parkerodynerus* gen. nov. differs from *Bohartodynerus* gen. n. by the truncate apical margin of the clypeus with rectangular lateral teeth in the female (Fig. 24), a larger flagellomere 11 in the male (Fig. 29), very large and deep cephalic foveae, separated by a distance significantly smaller than that between lateral ocelli in the female (Fig. 25), the pronotal carina, which is strongly developed and forming large acute angles at the anterolateral corners of the pronotum (Fig. 26), the absence of a distinct epicnemial carina, the presence of a sharp sub-basal carina bordering shallow concavity at the base of the mid femur in the male, the presence of a distinct basomedian longitudinal sulcus



Figs 23–31. *Parkerodynerus erythrogaster* (Bohart, 1939): 23–27 – female (23 – habitus, lateral view; 24 – clypeus; 25 – head, frontal view, arrow indicates a cephalic fovea; 26 – pronotum and mesonotum; 27 – tegula, arrow indicates the inner posterior angle); 28–31 – male (28 – clypeus; 29 – apex of antenna; 30 – mid leg beneath, arrow indicates the basal concavity; 31 – genitalia, dorsal view). Photos by M.Yu. Proshchalykin.

on the sternum 2, and a narrower aedeagus, which is rounded apically in the male (Fig. 12). The new genus is also somewhat similar to *Gymnomerus* due to its relatively slender body form and the structure of the pronotum but the latter taxon has the clypeus widely and deeply emarginate, mandible with a notch in both sexes, small and shallow cephalic foveae in the female, mid femur without a basal concavity in the male, the male posterior sterna without dense short pilosity, and different genitalia, particularly the aedeagus (Fig. 9).

DESCRIPTION. *Female.* Head about 1.1 as wide as long in frontal view; clypeus about 1.2 as wide as long, with apical truncation as wide as distance between antennal foveae, apical teeth rectangular (Fig. 24). Mandible without notch. Proboscis short, not reaches mid coxae. Maxillar palpi with 6 articles; labial palpi with 4 articles. Vertex approximately as long as upper portion of compound eye in dorsal view; cephalic foveae large and deep, separated by distance significantly smaller than that between lateral ocelli (Fig. 25). Anterior face of pronotum without distinct foveae; pronotal carina strongly developed, forming large acute angles at anterolateral corners of pronotum; pronotum beneath without acute angle anteriorly. Notauli sharply impressed, running entire length of scutum; parapsidal lines present on distal 2/3 of scutum; scutum evenly punctured (Fig. 26). Tegula small, nearly rounded posteriorly but with evident inner posterior angle where it adjoins scutum (Fig. 27); parategula very small. Epicnemial carina indistinct. Scutellum rather flat; axillary fossa deep. Metanotum rounded posteriorly. Propodeal shelf not developed. Propodeal concavity rather flat, its lateral borders rounded. Propodeal valvula entire. Second submarginal cell of fore wing not petiolate, with acute basal angle. Parastigma shorter than pterostigma. Tergum 1 hardly petiolate, without transverse carina at summit and without apical furrow. All metasomal terga without apical lamellae. Sternum 2 with distinct basomedian longitudinal sulcus. Black wasps with reddish pattern and mostly dark pilosity (Fig. 23).

Male. Resembles female but clypeus as wide as long, with apical emargination and acute apical teeth; clypeus covered with pale appressed setae besides erect dark pilosity (Fig. 28). Gena without projection behind mandible. Antenna with flagellomere 10 not much shorter than flagellomere 11; apex of antenna forming loose coiling (Fig. 29). Fore femur beneath without sharp edge. Mid coxa without projection; mid femur with sharp sub-basal carina bordering shallow concavity (Fig. 30). Sterna 3–6 with dense short pale pilosity. Genitalia as in Fig. 31. Aedeagus not very broad, rounded apically (Fig. 12).

ETYMOLOGY. The new genus-group name is dedicated to Frank D. Parker, an outstanding entomologist, for his significant contributions to the taxonomy and bionomics of the American eumenine wasps, including the bionomics of the species in this new genus. The gender is masculine.

SPECIES INCLUDED. *Parkerodynerus erythrogaster* (Bohart, 1939), **comb. n.** only.

DISTRIBUTION. Nearctic region (USA, Mexico).

Parkerodynerus erythrogaster **(Bohart, 1939), comb. n.**

Figs 12, 23–31

Monobia bicolor Provancher, 1888: 420–421, ♀ (type locality: “Anaheim” [USA: California]), holotype, ♀, in the collection of the Smithsonian National Museum of Natural History, Washington, D.C., USA. Junior secondary homonym in the genus *Odynerus* Latreille, 1802, nec de Saussure, 1855.

Odynerus erythrogaster Bohart, 1939: 81–82, replacement name for *Odynerus bicolor* (Provancher, 1888).

MATERIAL EXAMINED. **USA:** *California*: San Bernardino County, Redlands, 1 ♂, leg. F.R. Cole, ex coll. K.W. Cooper [FSCV]; San Diego County, Borrego Valley, Palm

Canyon, 1 ♀ (boring no. 2574B), 1 ♂ (boring no. 2565A), leg. F.D. Parker [FSCV]; Inyo County, Big Pine Creek, 7500′, 20.VI 1942, 1 ♂, leg. R.M. Bohart [CDFA]; Napa County, Samuel Spring, 13.V 1954, 1 ♀, leg. R.M. Bohart [CDFA]; Los Angeles County, Tanbark Flat, 25.VI 1958, 1 ♀, leg. R.M. Bohart [CDFA]; Santa Barbara County, Sunset Valley, 16.VI 1982, 2 ♀, leg. A.J. Gilbert [CDFA].

DISTRIBUTION. USA (Arizona, California), Mexico (Baja California).

REMARKS. The name *Monobia bicolor* being junior secondary homonym replaced before 1961 is permanently invalid (Art. 59.3 of ICZN, 1999).

BIONOMICS. Bohart (1951) was first who reported the nesting of this species in elderberry twigs (*Sambucus* spp.) while Parker & Bohart (1968) reported it utilizing pre-existing cavities of trap nests, but only Parker (1984) described the nests in detail. He studied a total of 207 nests; all of them were constructed in artificial borings in elderberry and raspberry (*Rubus* spp.) canes inserted vertically into the ground. The borings were of different diameters: 3 mm, 6 mm, and 9 mm; the narrow borings were widened and often lengthened by the female wasps, the medium borings were only lengthened but not widened, and the broad ones were not modified. The nests contained from 1 to 11 cells (mean values in different boring diameters were from 2.9 to 3.6) provisioned with gelechiid caterpillars. The partitions between the cells were made of packed sand while the closing plug was made of packed sand too but in some nests it contained also bits of debris. Apparently, the wasps did not use any liquid while constructed both the cell partitions and the closing plug.

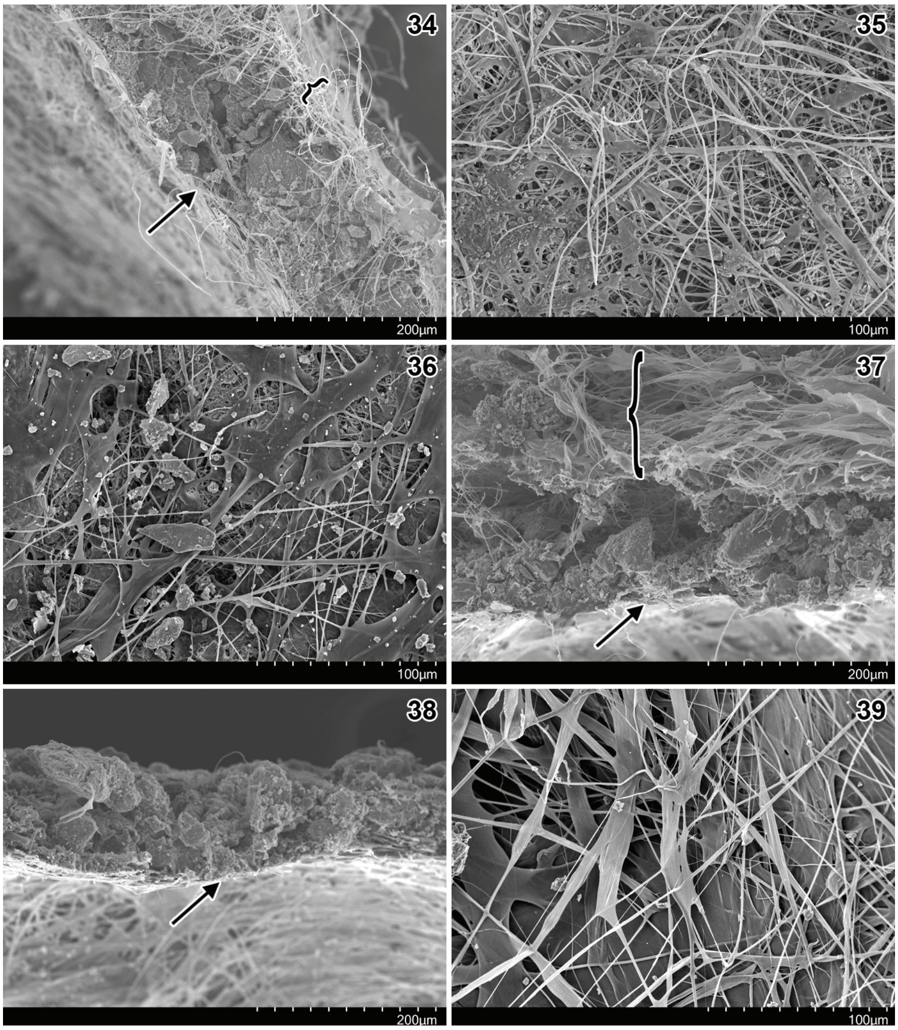




Figs 32–33. Cocoons of Odynerini s. str.: 32 – *Parkerodynerus erythrogaster* (Bohart, 1939), a whole cocoon with the opening made by the emerged wasp; 33 – *Paravespa rex* (von Schulthess, 1924), a dissected cocoon with some clayish substrate remaining laterally and at the bottom of the cell, arrow indicates the free part having a sandwich-like structure.

Parker (1984) described the cocoon of *P. erythrogaster*, which I also had an opportunity to study (Fig. 32). He paid an attention to the fact that this cocoon differed principally from the cocoons of most other representatives of the eumenine wasps, which constructed cocoons merely by lining the cell walls with silk. In the case of *P. erythrogaster*, the larva started cocooning with making a bag-like case of silk that was not firmly attached to the cell walls. Then, it removed pieces of sand from the partition above the cell and used them to line the inside of the case. After that, the larva finished the inside of the cocoon by depositing the inner layer of silk over the sand particles. Dissection of a complete cocoon of *P. erythrogaster* confirmed its sandwich-like structure (Fig. 34) described by Parker (1984). The outer layer, looked from the outside like a whitish cobweb (Fig. 32), consisted of a chaotic interweaving of silk strands (Fig. 35). The thickest middle layer was represented by sand particles (Fig. 34). The thinnest inner layer consisted of mostly broad strands and presumably airtight films of silk, with an inclusion of some sand microparticles, apparently penetrating there from the middle layer (Fig. 36).

Parker (1984) also reported that the species was univoltine and hybernating at the prepupal stage; the sex ratio was female-biased (1.2: 1). He also provided data on the nest associates: predators and brood parasites. An unusual feature was a low immature mortality: about 22% (14.8% due to the nest associates and 7.1% due to unknown reasons).



Figs 34–39. Cocoons of Odynerini s. str.: 34–36 – *Parkerodynerus erythrogaster* (Bohart, 1939) (34 – dissection of a lateral part; 35 – detached outer layer from the inside; 36 – inner layer from the inside); 37–39 – *Odynerus* (*Odynerus*) *spinipes* (Linnaeus, 1758) (37 – dissection of a free part; 38 – dissection of a lateral part with some clayish substrate forming the middle layer; 39 – inner layer from the inside). Arrows indicate the inner layer; figure parentheses indicate the outer layer.

DISCUSSION

There are no doubts that either *Bohartodynerus* or *Parkerodynerus* cannot be merged into the genus *Odynerus*. They are even more different from *Odynerus* than some Palaearctic genera (first of all, *Gymnomerus*) which have been already separated from it by Blüthgen (1938a, 1938b, 1939, 1941). Another question can be arisen: why *Bohartodynerus* and *Parkerodynerus* were described above as two genera instead of a single genus for all the members of the "red" complex? The answer is that there are no strong evidences of their sister phylogenetic relationships. As was stated above, *Bohartodynerus* and *Parkerodynerus* share the following characters which distinguish both genera from *Odynerus*: a narrow apical margin of the clypeus, the absence of distinct pronotal foveae, sharply impressed notauli and distinct parapsidal lines, the tegula with a small but evident inner posterior angle where it adjoins the scutum, a dense short pilosity of the posterior sterna in the male, and a reddish pattern. Most of these characters are of plesiomorhic state (such as sharply impressed notauli or the tegula shape, Carpenter & Cumming, 1985) or cannot be considered as apomorphic without doubts (such as clypeal shape or body coloration). The only possible clear synapomorphy is a dense short pilosity of the posterior sterna in the male but it is also arizen independently in *Paragymnomerus* and *Tropidodynerus*, as well as several representatives of the *Pterocheilus* group. As for the similar color pattern of the two newly described genera, it is not surprising since it can be merely a case of the Müllerian mimicry that is rather common in the eumenine wasps (Garcete-Barrett, 2014; Selis, 2020).

Therefore, I prefer to recognize *Bohartodynerus* and *Parkerodynerus* as two separate genera until they are studied phylogenetically (preferably involving molecular data) despite the opinion that the "proliferation of genera is merely the sort of extreme splitting" (Carpenter & Garcete-Barrett, 2002: 52). If further studies will show their sister position, they can be treated as subgenera of a single genus. The differences between *Bohartodynerus* and *Parkerodynerus* are, however, at least not less than those between *Odynerus* and *Gymnomerus*. In both pairs of these genera there are differences in the female clypeus and cephalic foveae, as well as the male legs and genitalia (they are, however, quite similar in *Odynerus* and *Gymnomerus*, while very different in *Bohartodynerus* and *Parkerodynerus*). Unfortunately I did not have a chance to examine the genitalia of *Bohartodynerus* but the drawing in Bohart (1939: 79, fig. 3) allows to consider them different enough from those of both *Odynerus* and *Parkerodynerus*.

Different kinds of cephalic foveae and distinct notauli are also present in the genus *Symmorphus* Wesmael, 1836 (Cumming, 1989) but it is hardly possible that the latter one is closely related to *Bohartodynerus* and *Parkerodynerus*. It rather means that both groups (*Symmorphus* and the "red" complex of two newly described genera) are generalized (posses a significant number of plesiomorhic characters) that is confirmed by the basal phylogenetic position of *Symmorphus* within its clade on the "molecular" cladograms (Bank *et al*., 2017; Piekarski *et al*., 2018).

It is worthy to mention, that each genus in the *Odynerus* group of the tribe Odynerini s. str. has their peculiar nesting bionomics and there are no genera sharing all the main behavioral characters of the females (Table 1). At the same time, species within each genus have very similar bionomics; they differ mainly in the ecological preferences of a certain type of landscape or a certain species of prey within the given prey group, as well as in the minor details of the nest parameters. This is true for several species of *Odynerus*, which were studied bionomically (e. g., Miotk, 1979; Bohart *et al*., 1982; Schaber, 1985; Haeseler, 1997; Fateryga, 2013), two studied species of *Paragymnomerus* (Móczár, 1939; Fateryga, 2018), four studied species of *Paravespa* (Blüthgen, 1957; Gess & Gess, 1988; Fateryga & Ivanov,

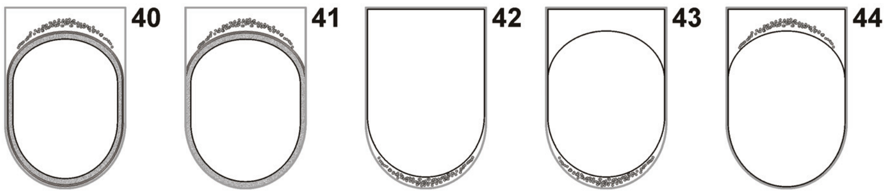
2013), and two studied species of *Tropidodynerus* (Ferton, 1895; Arens, 1999; Fateryga, 2009). The genus *Gymnomerus* is monotypic and has very specific, unique nesting habits (e. g., Fateryga, 2012), that is true for the genus *Parkerodynerus* as well. Neither *Bohartodynerus* nor *Parkerodynerus* can be treated as members of the genus *Odynerus* according to their ethology, and the differences between these two newly described taxa are also enough to recognize them as separate genera (Table 1).

Table 1. Comparison of the nesting habits of the genera in *Odynerus* group of Odynerini s. str.

Genus	Nesting substrate	Nest structure	Liquid use	Prey
Bohartodynerus	Pre-existing cavities in twigs* (and probably stone caverns)	No turret, closing plug made of glued gravel	Apparently nectar (to glue gravel)	Unidentified Lepidoptera
Parkerodynerus	Pre-existing cavities in twigs*	No turret, closing plug and partitions made of packed soil	No liquid is apparently used	Lepidoptera: Gelechiidae
Odynerus	Ground	Curved or straight turret, closing plug and partitions made of mud	Water (to moisten the ground and prepare mud)	Free-living Coleoptera: Curculionidae
Gymnomerus	Pre-existing cavities in twigs*	No turret, closing plug made of packed soil, cell bottoms and walls made of mud	Water (to prepare mud)	Free-living Coleoptera: Curculionidae
Paragymnomerus	Ground	Curved turret, closing plug and partitions made of mud	Water (to moisten the ground and prepare mud)	Hymenoptera: Pamphilioidea
Paravespa	Ground	Either curved or funnel-shaped turret, closing plug and partitions made of mud	Water (to moisten the ground and prepare mud)	Lepidoptera: Noctuidae
Tropidodynerus	Ground	No turret, the entrance is temporary closed with mud pellets and then with a mud plug	Water (to moisten the ground and prepare mud)	Endophytic Coleoptera: Curculionidae

* – can be often modified (enlarged) by the female wasp. The data on most of the genera (except first two) are from my previous papers (Fateryga, 2009, 2012, 2013, 2018; Fateryga & Ivanov, 2013) and references therein.

In my previous papers, I described cocoons of *Tropidodynerus* and *Gymnomerus* as consisting of a single thick layer (Fateryga, 2009, 2012). Then, I described cocoons of *Odynerus*, *Paravespa*, and *Paragymnomerus* (Fateryga, 2013, 2018; Fateryga & Ivanov, 2013) as consisting of an outer silk layer at its free part and an inner thick layer "made with the help of fluid secretion penetrating into the cell walls and making them durable and water-proof" (e. g., Fateryga & Ivanov, 2013: 595; Fateryga, 2018: 437). That was not true. Detailed re-examination of the cocoons of *Paravespa* (Fig. 33) and *Odynerus* (Figs 37–39) revealed that they actually had a sandwich-like structure (Fig. 37), similar to that in the cocoon of *Parkerodynerus*, but present only at the free part (= proximal end) of the cocoon instead over its whole surface (cf. Fig. 40 with Fig. 41). Therefore, cocoons of *Paravespa* and *Odynerus* cannot be easily detached from the substrate (Fig. 33). Their outer layer is made of a loose chaotic interweaving of silk strands and films (Fig. 37) in the form of a convex meniscus at a distance from the inner surface of the outer cell partition. Thus, the outer layer is present only at the proximal end of the cocoon while the middle layer (consisting of soil, Figs 37, 38) and the inner one (consisting of mostly broad silk strands, Fig. 39) are present over the whole cocoon surface (Fig. 41). Such cocoon structure is apparently peculiar also to *Gymnomerus*, *Paragymnomerus*, and *Tropidodynerus*.



Figs 40–41. Schematic plans of the eumenine wasp cocoons: 40 – *Parkerodynerus* (the whole cocoon have a sandwich-like structure, its outer layer is loose, prey feces are supposed to be above the cocoon, the inner surface of the cell plug is not covered with silk); 41 – *Odynerus*, *Paravespa*, and probably most other Odynerini s. str. (only the free part have a sandwich-like structure, its outer layer is loose, prey feces are above the cocoon, the inner surface of the cell plug is not covered with silk); 42–44 – most other Eumeninae s. str. (42 – one layer, prey feces are below the cocoon; 43 – two layers, prey feces are below the cocoon; 44 – two layers, prey feces are between them).

One more common trait of the cocoons of *Parkerodynerus* and other members of the *Odynerus* group is that the inner surface of the outer cell partition is not covered with silk (Figs 40, 41). Cocoons of most other wasps in the subfamily Eumeninae s. str. completely cover the inner surface of the cell including the outer partition (Figs 42–44). They can be also consisted of several layers (Figs 43, 44) but these layers are made of silk only; none of such cocoons have a sandwich-like structure involving sand or soil (Figs 43, 44). Therefore, cocoons of *Parkerodynerus* are outstanding among other Odynerini s. str. but the whole group of Odynerini s. str., in its turn, differs enough from the remaining eumenine wasps in its habits, particularly the cocooning behavior.

ACKNOWLEDGEMENTS

I thank to A.S. Lelej and V.M. Loktionov for loaning the specimens from FSCV. I am also greatly indebted to K.A. Williams (Sacramento, USA) and M.Yu. Proshchalykin (Vladivostok, Russia) for providing high quality photos of the specimens from CDFA and FSCV. The work was a part of the State research project No. AAAA-A19-119012490044-3.

REFERENCES

Arens, W. 1999. Zum Verhalten von *Tropidodynerus interruptus* (Brullé 1832) (Vespoidea, Eumenidae) und seines Brutparasiten *Chrysis jaxartis* Sem. am Nest. *Linzer Biologische Beiträge*, 31(1): 147–158.

Bank, S., Sann, M., Mayer, C., Meusemann, K., Donath, A., Podsiadlowski, L., Kozlov, A., Petersen, M., Krogmann, L., Meier, R., Rosa, P., Schmitt, T., Wurdack, M., Liu, S., Zhou, X., Misof, B., Peters, R.S. & Niehuis, O. 2017. Transcriptome and target DNA enrichment sequence data provide new insights into the phylogeny of vespid wasps (Hymenoptera: Aculeata: Vespidae). *Molecular Phylogenetics and Evolution*, 116: 213–226. DOI: https://doi.org/10.1016/j.ympev.2017.08.020

Barlow, S.E. & Pavlik, B.M. 2017. Estimating the spatial dimensions of *Astragalus holmgreniorum* mutualisms. I. Pollinator visitation and behaviors along a seed set gradient: Report to the State of Utah Department of Natural Resources Endangered Species Recovery Program. Nature Conservancy Utah Field Office, Salt Lake City, 25 pp.

Blüthgen, P. 1938a. Systematisches Verzeichnis der Faltenwespen Mitteleuropas, Skandinaviens und Englands. *Konowia*, [1937], 16: 270–295.

Blüthgen, P. 1938b. Beiträge zur Kenntnis der paläarktischen Eumeniden (Hym. Vespidae). *Deutsche Entomologische Zeitschrift*, 1938(2): 434–495. DOI: https://doi.org/10.1002/mmnd.193819380208

Blüthgen, P. 1939. Beiträge zur Kenntnis der paläarktischen und einiger äthiopischer Faltenwespen (Hym. Vespidae). *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen*, 2(3): 233–267.

Blüthgen, P. 1941. Die Untergattungen *Hoplomerus* s. str. und *Monoplomerus* der Gattung *Hoplomerus* Westwood (Hym. Vespidae Eumenidinae). *Archiv für Naturgeschichte*, 10(3): 305–344.

Blüthgen, P. 1957. Zur Lebensweise der *Paravespa*-Arten. *Zoologischer Anzeiger*, 159: 33–34.

Bohart, G.E., Parker, F.D. & Tepedino, V.J. 1982. Notes on the biology of *Odynerus dilectus* (Hymenoptera: Eumenidae), a predator of the alfalfa weevil, *Hypera postica* (Coleoptera: Curculionidae). *Entomophaga*, 27(1): 23–31. DOI: https://doi.org/10.1007/BF02371934

Bohart, R.M. 1939. Taxonomy of the typical subgenus *Odynerus* in North America (Hymenoptera, Vespidae). *Pan-Pacific Entomologist*, 15(2): 76–84.

Bohart, R.M. 1951. Family Vespidae. P. 875–907. *In*: Muesebeck, C.F.W., Krombein, K.V. & Townes, H. (Eds.). *Hymenoptera of America north of Mexico. Synoptic catalog*. United States Government Printing Office, Washington. (Agriculture Monograph No. 2). DOI: https://doi.org/10.5962/bhl.title.65057

Carpenter, J.M. 1982. The phylogenetic relationship and natural classification of the Vespoidea (Hymenoptera). *Systematic Entomology*, 7(1): 11–38. DOI: https://doi.org/10.1111/j.1365-3113.1982.tb00124.x

Carpenter, J.M. & Cumming, J.M. 1985. A character analysis of the North American potter wasps (Hymenoptera: Vespidae; Eumeninae). *Journal of Natural History*, 19(5): 877–916. DOI: https://doi.org/10.1080/00222938500770551

Carpenter, J.M. & Garcete-Barrett, B.R. 2002. A key to the Neotropical genera of Eumeninae (Hymenoptera: Vespidae). *Boletín del Museo Nacional de Historia Natural del Paraguay*, 14(1–2): 52–73.

Cumming, J.M. 1989. Classification and evolution of the eumenine wasp genus *Symmorphus* Wesmael (Hymenoptera: Vespidae). *Memoirs of the Entomological Society of Canada*, 148: 5–168. DOI: https://doi.org/10.4039/entm121148fv

Fateryga, A.V. 2009. The observations on the nesting behavior of the solitary wasp *Tropidodynerus interruptus* (Brullé, 1832) (Hymenoptera, Vespidae, Eumeninae) in Crimea. *Euroasian Entomological Journal*, 8(4): 381–385 + 380 + VI. [In Russian]

Fateryga, A.V. 2012. Nesting of the wasp *Gymnomerus laevipes* (Hymenoptera, Vespidae) in the Crimea. *Vestnik Zoologii*, 46(3): 229–238. [In Russian]

Fateryga, A.V. 2013. Nesting biology of *Odynerus albopictus calcaratus* (Morawitz, 1885) and *Odynerus femoratus* de Saussure, 1856 (Hymenoptera: Vespidae: Eumeninae). *Journal of Insects*, 597583. DOI: https://doi.org/10.1155/2013/597583

Fateryga, A.V. 2018. Nesting biology of *Paragymnomerus signaticollis tauricus* (Kostylev, 1940) (Hymenoptera: Vespidae: Eumeninae). *Zootaxa*, 4378(3): 429–441. DOI: https://doi.org/10.11646/zootaxa.4378.3.10

Fateryga, A.V. & Ivanov, S.P. 2013. Nesting biology of *Paravespa rex* (von Schulthess 1924) (Hymenoptera: Vespidae: Eumeninae) in the Crimea, Ukraine. *Zootaxa*, 3721(6): 589–600. DOI: https://doi.org/10.11646/zootaxa.3721.6.5

Fateryga, A.V. & Podunay, Yu.A. 2018. Nesting and biology of *Alastor mocsaryi* (Hymenoptera, Vespidae: Eumeninae). *Entomological Review*, 98(8): 1006–1016. DOI: https://doi.org/10.1134/S0013873818080079

Fateryga, A.V., Popovich, A.V., Podunay, Yu.A. & Fateryga, V.V. 2020. First data on the bionomics of *Leptochilus* (*Euleptochilus*) *limbiferus* (Morawitz, 1867) (Hymenoptera: Vespidae: Eumeninae), with taxonomic notes and new records. *Zootaxa*, 4851(2): 289–304. DOI: https://doi.org/10.11646/zootaxa.4851.2.4

Ferton, C. 1895. Observations sur l'instinct de quelques Hyménoptères du genre *Odynerus* Latreille. *Actes de la Société Linnéenne de Bordeaux*, 48: 219–230.

Garcete-Barrett, B.R. 2014. *Stenonartonia tekoraava* sp. nov. (Hymenoptera: Vespidae: Eumeninae), a new member of a typical Amazonian mimicry ring. *Zootaxa*, 3860(1): 97–100. DOI: https://doi.org/10.11646/zootaxa.3860.1.7

Gess, F.W. & Gess, S.K. 1988. A contribution to the knowledge of the ethology of the genera *Parachilus* Giordani Soika and *Paravespa* Radoszkowski (Hymenoptera: Eumenidae) in southern Africa. *Annals of the Cape Provincial Museums. Natural History*, 18(3): 57–81.

Haeseler, V. 1997. Die *Odynerus*-Arten *O. eburneofasciatus* Dusmet 1903, *O. antigai* Dusmet 1903 sowie *O. annulicornis* Blüthgen 1956 und zur Biologie von *O. eburneofasciatus* Dusmet 1903 (Vespoidea: Eumenidae). *Linzer Biologische Beiträge*, 29(1): 151–166.

Hermes, M.G., Melo, G.A.R. & Carpenter, J.M. 2014. The higher-level phylogenetic relationships of the Eumeninae (Insecta, Hymenoptera, Vespidae), with emphasis on *Eumenes* sensu lato. *Cladistics*, 30(5): 453–484. DOI: https://doi.org/10.1111/cla.12059

International Commission on Zoological Nomenclature (ICZN). 1999. *International Code of Zoological Nomenclature. Fourth Edition.* ITZN, London, i–xxx + 306 pp. DOI: https://doi.org/10.5962/bhl.title.50608

Krombein, K.V. 1979. Superfamily Vespoidea. P. 1469–1522. *In*: Krombein, K.V., Hurd, P.D., Smith, D.R. & Burks, B.D. (Eds). *Catalog of Hymenoptera in America north of Mexico. Vol. 2: Apocrita (Aculeata)*. Smithsonian Institution Press, Washington.

Miotk, P. 1979. Zur Biologie und Ökologie von *Odynerus spinipes* (L.) und *O. reniformis* (Gmel.) an den Losswanden des Kaiserstuhls (Hymenoptera: Eumenidae). *Zoologische Jahrbücher. Abteilung für Systematik Ökologie und Geographie der Tiere*, 106(3): 374–405.

Móczár, L. 1939. Beobachtungen über den Nestbau einiger *Odynerus*-Arten. *Zoologischer Anzeiger*, 125: 70–80.

Parker, F.D. 1966. A revision of the North American species in the genus *Leptochilus* (Hymenoptera: Eumenidae). *Miscellaneous Publications of the Entomological Society of America*, 5: 151–229.

Parker, F.D. 1984. Nests and nest associates of two “red” *Odynerus* wasps (Hymenoptera: Eumenidae). *Journal of the Kansas Entomological Society*, 57(3): 521–525.

Parker, F.D. & Bohart, R.M. 1968. Host-parasite associations in some twig-nesting Hymenoptera from western North America. Part II. *Pan-Pacific Entomologist*, 44(1): 1–6.

Piekarski, P.K., Carpenter, J.M., Lemmon, A.R., Lemmon, E.M. & Sharanowski, B.J. 2018. Phylogenomic evidence overturns current conceptions of social evolution in wasps (Vespidae). *Molecular Biology and Evolution*, 35(9): 2097–2109. DOI: https://doi.org/10.1093/molbev/msy124

Provancher, L. 1885–1889. *Additions et corrections au Volume II de la Faune Entomologique du Canada traitant des Hyménoptères.* C. Darveau, Québec. (1885) 1–14; (1886) 15–164; (1887) 165–272; (1888) 273–440; (1889) 441–475, errata. DOI: https://doi.org/10.5962/bhl.title.46411

Rohwer, S.A. 1915. Descriptions of new species of Hymenoptera. *Proceedings of the United States National Museum*, 49: 205–249.

Schaber, B.D. 1985. Observations on nesting behavior and turret construction by *Odynerus dilectus*. *Canadian Entomologist*, 117(9): 1159–1161. DOI: https://doi.org/10.4039/Ent1171159-9

Selis, M. 2020. On generic placement of *Odynerus dictatorius* Giordani Soika and its mimicry ring (Hymenoptera: Vespidae: Eumeninae). *Zootaxa*, 4845(1): 83–96. DOI: https://doi.org/10.11646/zootaxa.4845.1.6

Yamane, Sk. 1990. A revision of the Japanese Eumenidae (Hymenoptera, Vespoidea). *Insecta Matsumurana. New Series*, 43: 1–189.